

# Review of the Nudibranch Genus *Melibe* (Opisthobranchia: Dendronotacea) with Descriptions of Two New Species

by

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**Abstract.** Two new species of the genus *Melibe* are described. *Melibe liltvedi* sp. nov. is known from the Atlantic coast of South Africa while *M. megaceras* sp. nov. is recorded from the Hawaiian Islands. The morphologies of *M. leonina* (Gould, 1852), *M. pilosa* Pease, 1860, and *M. rosea* Rang, 1829, are also described. A review of morphological variability within the genus is provided.

## INTRODUCTION

THE DENDRONOTACEAN GENUS *Melibe* consists of 13 described species from throughout the world. Most species have been superficially described, with an emphasis on external morphological features. For example, the reproductive morphology of the type species, *Melibe rosea* Rang, 1829, remains largely undescribed. Several species, *M. capucina* Bergh, 1875, *M. engeli* Risbec, 1937, *M. maugiana* Burn, 1960, *M. ocellata* Bergh, 1888, and *M. rangi* Bergh, 1875, are known only from their original descriptions. Collections of two apparently undescribed species from South Africa and Hawaii have prompted a review of the genus in order that adequate morphological comparisons can be made.

### Family TETHYIDAE

#### *Melibe* Rang, 1829

#### *Melibe leonina* (Gould, 1852)

(Figures 1A, 2, 8D, 9C)

*Chioraera leonina* GOULD, 1852:310, pl. 26, fig. 404.

*Melibe leonina* (Gould, 1852): BERGH, 1875:364.

*Melibe pellucida* BERGH, 1904:11, pl. 4, figs. 33, 34;  
O'DONOGHUE, 1922:148.

*Chioraera dalli* HEATH, 1917:137, pls. 11-13; O'DONOGHUE,  
1922:148.

*Melibe dalli* (Heath, 1917): ODHNER, 1936:1117.

**Material:** Three specimens, California Academy of Sciences, CASIZ 061504, collected intertidally, on *Zostera marina* Linnaeus, Limantour Estero, Marin County, Cal-

ifornia, 28 December 1967, T. M. Gosliner. One specimen, collected from 16 m depth, on outer side of breakwater, Monterey Harbor, Monterey Bay, Monterey County, California, 4 August 1978, T. M. Gosliner.

**Description: External morphology:** The preserved specimens are a maximum of 50 mm in length. The living animals (Figure 1A) are translucent yellowish with small opaque white spots present on the notum. A single specimen photographed by the author in Friday Harbor, Washington, had large, scattered opaque white spots, approximately 2 mm in diameter. The large circular oral hood contains an inner and outer row of papillae along its entire margin. The papillae on the outer row of the hood are significantly longer than those of the inner row. The rhinophore sheaths (Figure 8D) are relatively large and are flattened. The rhinophores are perfoliate with 4-6 lamellae. There are 3-6 cerata on either side of the body. Each ceras (Figure 9C) is flattened and ovoid in shape. The anteriormost cerata are largest. The anus is located anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The single gonopore is ventral to the anteriormost right ceras. The foot is relatively narrow with an entire anterior margin.

**Digestive system:** The buccal mass is thick, muscular, and devoid of jaws or a radula. A short salivary gland is present near the middle of either side of the buccal mass. From the posterior end of the buccal mass a short esophagus expands into the muscular stomach. The stomach contains no chitinous plates. On the dorsal side of the stomach is a pair of glandular folded pouches, each of

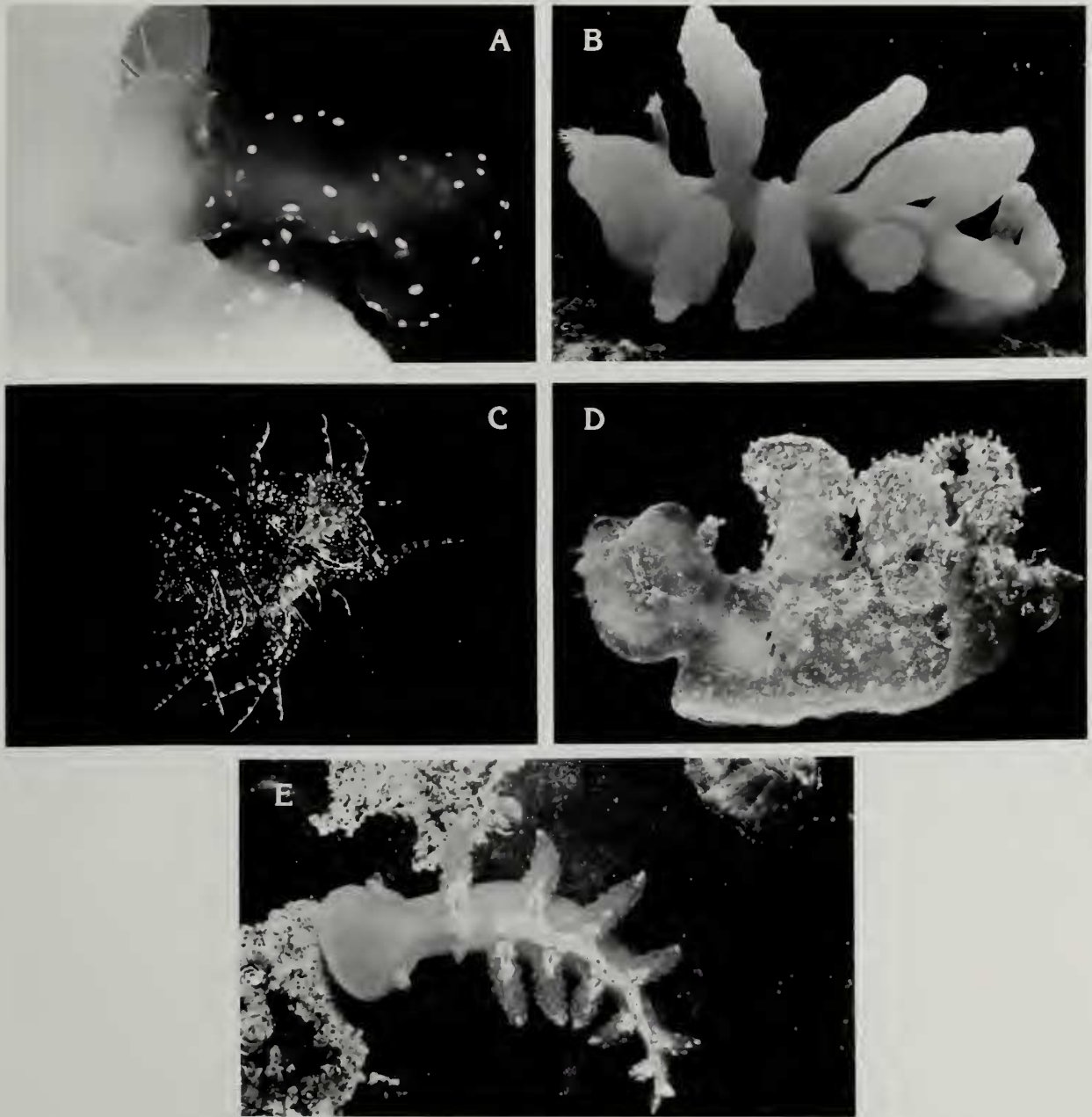


Figure 1

Living animals. A. *Melibe leonina* (Gould, 1852). B. *Melibe liltvedi* sp. nov. C. *Melibe megaceras* sp. nov. D. *Melibe pilosa* Pease, 1860. E. *Melibe rosea* Rang, 1829.

which expands into digestive gland ducts. The right duct is undivided and extends to the base of the anteriormost right ceras. The left duct bifurcates, with an anterior branch joining the base of the anteriormost left ceras and a posterior branch extending to the bulk of the digestive gland. This digestive gland mass branches to each of the posterior cerata. The posteroventral portion of the stomach is a lobed glandular region that is contiguous with the

intestine. The intestine extends ventrally and recurves dorsally, terminating at the anus.

**Central nervous system** (Figure 2A): The arrangement of ganglia is identical to that described for *Melibe megaceras*, with a few notable exceptions. The cerebral ganglia are bilobed anteriorly and there is a prominent bulge near their posteromedial margin. Similarly, the pedal ganglia are prominently bilobed.

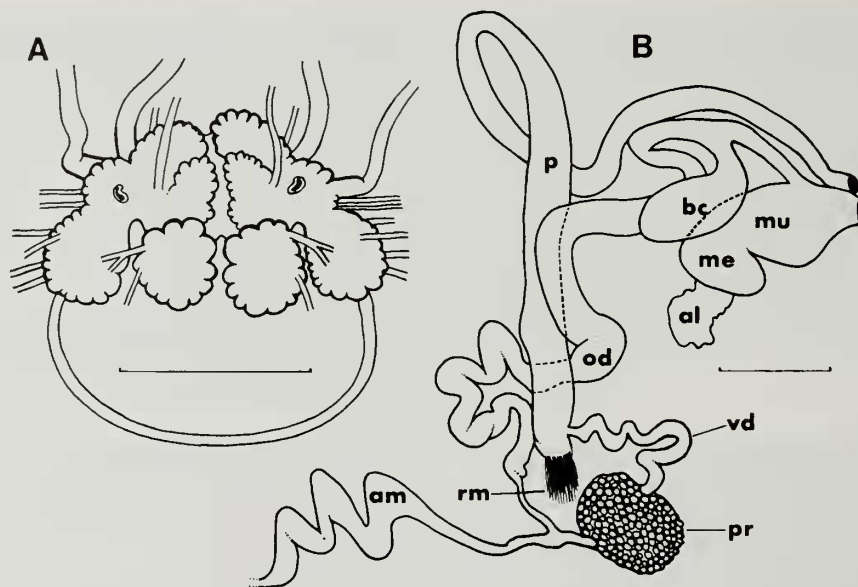


Figure 2

*Melibe leonina* (Gould, 1852). A. Central nervous system, scale = 1.0 mm. B. Reproductive system, scale = 2.0 mm. al = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; p = penis; pr = prostate; rm = retractor muscle; vd = vas deferens.

**Reproductive system** (Figure 2B): All of the reproductive organs are elongate. The ampulla is narrow with approximately four convolutions. It divides distally into the vas deferens and the oviduct. The oviduct abruptly widens and consists of numerous convolutions. It continues to widen distally and curves adjacent to the penis. The oviduct contains numerous tubules within its walls. Near its base, the oviduct branches into a short duct which leads to the pyriform bursa copulatrix. The oviduct continues distally and joins the female genital opening. The albumen gland is situated near the proximal limit of the female gland mass. It merges with the membrane gland and the larger mucous gland. The mucous gland joins the oviduct at the female gonopore. The vas deferens enters the prostate a short distance after the branching of the ampulla. The prostate is spherical and consists of numerous small flocculent bodies. From the distal end of the prostate the vas deferens again emerges as a muscular, highly convoluted ejaculatory portion. The vas deferens enters the penial sac laterally. From the posterior end of the penial sac is attached a short penial retractor muscle. The penis is exceedingly elongate and flattened for most of its length. It is unarmed and terminates at the male gonopore.

**Natural history:** Specimens have been collected from the intertidal region on eel grass, *Zostera marina* Linnaeus, to a depth of 18 m, where they frequently are encountered on the kelp *Macrocystis pyrifera* (Linnaeus) Agardh. Gut contents of specimens collected from Limantour Estero indicate that *Melibe leonina* feeds on gammaridean and

caprellid amphipods. AJESKA & NYBAKKEN (1976) have studied in detail the biology of *Melibe leonina*.

**Distribution:** Specimens have been collected from Dall Island, Alaska, to Punta Abrejos, on the Pacific coast of Baja California, and into the Gulf of California (McDONALD, 1983).

*Melibe liltvedi* Gosliner, sp. nov.

(Figures 1B, 3, 8E, 9D, 10D)

**Type material:** Holotype: South African Museum, Cape Town, SAM A35776, collected in 20 m of water, Bakoven, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 21 March 1981, W. R. Liltved.

Paratypes: SAM A35773, one specimen, collected in 18 m of water, Hottentot's Huisie, Oudekraal, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 18 February 1981, W. R. Liltved. SAM A35772, one specimen, collected in 25 m depth, Llandudno, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 17 September 1982, W. R. Liltved.

**Etymology:** This species is named for my friend and colleague, Bill Liltved, for his assistance in all aspects of my opisthobranch research in southern Africa.

**Description: External morphology:** The preserved specimens (Figure 3A) range from 19 to 55 mm in length. When alive the animals (Figure 1B) are uniformly opaque white in color. The entire, circular oral hood is large

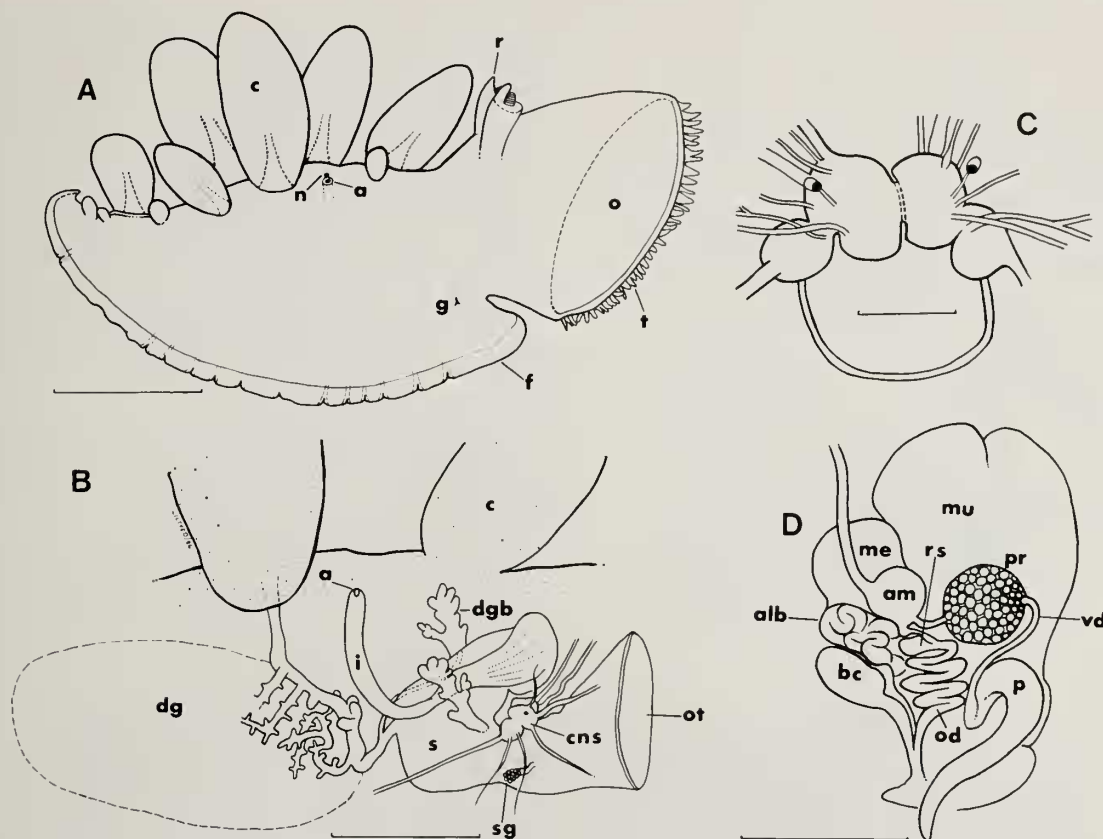


Figure 3

*Melibe liltvedi* sp. nov. A. Right lateral view of juvenile preserved specimen, scale = 3.0 mm. a = anus; c = ceras; f = foot; g = gonopore; n = nephroproct; o = oral hood; r = rhinophore; t = tentacle. B. Digestive system, scale = 2.0 mm. a = anus; c = ceras; cns = central nervous system; dg = digestive gland; dgb = digestive gland branch; i = intestine; ot = oral tube; s = stomach; sg = salivary gland. C. Central nervous system, scale = 1.0 mm. D. Reproductive system, scale = 1.0 mm. alb = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; p = penis; pr = prostate; rs = receptaculum seminis; vd = vas deferens.

relative to the remainder of the body. It contains 2 to 3 rows of elongate papillae along its margin. The innermost row contains the longest papillae. The rhinophore sheath (Figure 8E) is simple, with an expanded margin that possesses a single triangular papilla at its posterior end. The rhinophores are perfoliate with 6 or 7 lamellae. There are 5 or 6 cerata on either side of the body. Each ceras (Figure 9D) is pyriform with low tubercles scattered over its surface, giving the entire ceras a nodular appearance. The anus is situated on the right side of the body, anterior to the second ceras. The nephroproct is immediately dorsal to the anus. The single gonopore is ventral to the anteriormost right ceras. The anteriorly rounded foot is narrow relative to the rest of the body.

**Digestive system** (Figure 3B): The buccal mass is muscular throughout its length. No vestige of jaws or a radula is present in any of the three specimens examined. Extending from the posterior portion of either side of the

buccal mass is a short, lobate salivary gland. From the posterior limit of the buccal mass the short esophagus widens into the stomach. The posterior end of the stomach is muscular and lined with 5 or 6 chitinous plates (Figure 10D). There is a single glandular duct emerging from either side of the stomach. The right duct enters the base of the anteriormost right ceras. The left duct is bifurcate, with the anterior branch entering the anteriormost left ceras and the posterior duct giving rise to the bulk of the lobate digestive gland. The posterior digestive gland branches to the base of each of the posterior cerata. The intestine emerges from the posterodorsal end of the stomach, curves ventrally, recurves dorsally, and terminates at the anus.

**Central nervous system** (Figure 3C): The arrangement of ganglia within the nervous system is identical to that described for *Melibe megaceras*. The ganglia are smooth in texture and rounded.



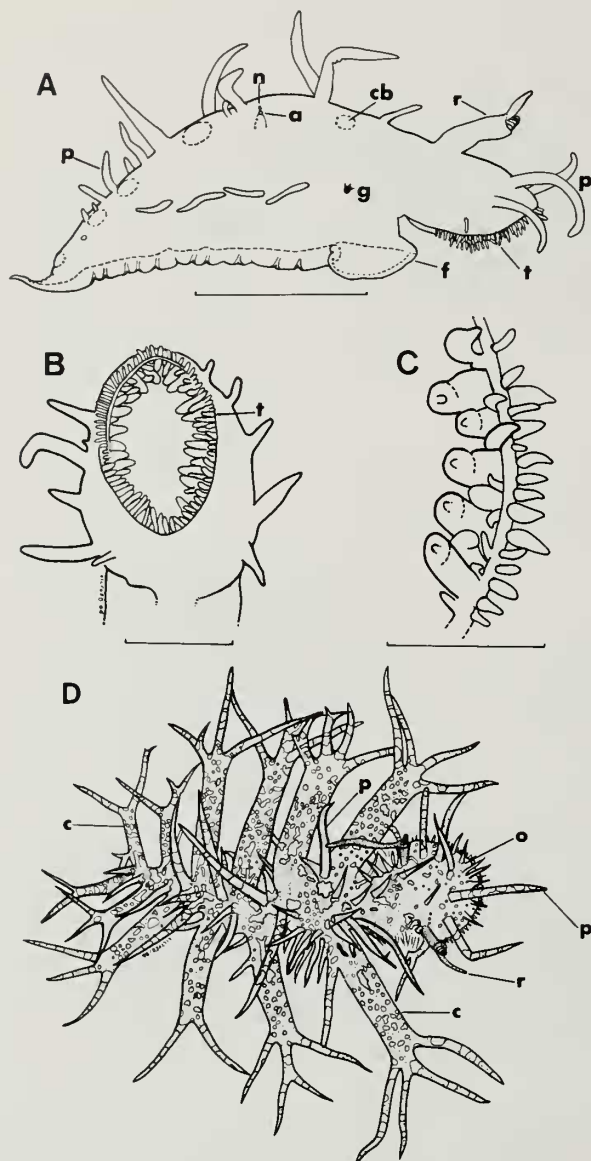


Figure 4

*Melibe megaceras* sp. nov. A. Right lateral view of preserved animal, scale = 10 mm. a = anus; cb = ceratal base; f = foot; g = gonopore; n = nephroproct; p = papilla; r = rhinophore; t = tentacles. B. Oral hood, scale = 2.5 mm. t = tentacles. C. Detail of oral hood, scale = 2.0 mm. D. Dorsal view of living animal. c = ceras; o = oral hood; p = papilla; r = rhinophore.

**Reproductive system** (Figure 3D): The preampullary duct is elongate and expands into an S-shaped ampulla. The ampulla bifurcates into the oviduct and vas deferens. The oviduct is narrow and convoluted, widening gradually more distally. The proximal end enters a blind sac that probably functions as a short receptaculum seminis. More distally the oviduct joins the duct of the bursa copulatrix near the bursa's junction with the common genital

atrium. The bursa copulatrix is pyriform, with a relatively short duct in all three specimens examined. The female gland mass is well developed. The albumen gland is the most proximal portion, consisting of several large ovoid bodies. The membrane gland is immediately distal to the albumen gland and is highly folded. The mucous gland forms the largest portion of the nidamental glands. The vas deferens continues proximally from its junction with the oviduct and ampulla. After a short distance it enters the globular prostate gland, which is composed of numerous large spherical bodies. The vas deferens emerges again from the prostate as a wider, muscularized ejaculatory duct, which gradually widens into the curved, conical penis.

**Natural history:** Specimens have been found from 15 to 45 m depth, where they generally inhabit crevices near the bases of cliffs. Frequently, they have been seen in small aggregations of 3–5 individuals.

**Distribution:** Animals have been found only along the Atlantic coast of the Cape Peninsula from Bakoven to Haut Bay.

*Melibe megaceras* Gosliner, sp. nov.

(Figures 1C, 4, 5, 8G, 9F, 10E)

*Melibe* sp.: KEMPF, 1984.

**Type material:** Holotype: California Academy of Sciences, CASIZ 061507, collected in 3 m of water, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 12 February 1986, by Terrence M. Gosliner.

Paratypes: CASIZ 061508, 14 specimens, collected in 3 m of water, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 12 and 13 February 1986, Terrence M. Gosliner and Michael T. Ghiselin. CASIZ 061509, 6 specimens, collected in 3 m of water, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 15 February 1986, Terrence M. Gosliner and Michael T. Ghiselin.

**Etymology:** The epithet *megaceras* refers to the large cerata, which may be almost as long as the body proper.

**Description: External morphology:** The preserved animals (Figure 4A) are a maximum of 30 mm in length. The living animals (Figures 1C, 4D) are translucent white with brown spots, which represent concentrations of zooxanthellae. Alternating bands of brown and opaque white pigment are present on the rhinophores, cerata, and on the elongate papillae on the head, notum, and sides of the body. Irregularly spaced on the body and cerata are patches of opaque white pigment. The oral hood (Figure 4B) is circular and entire along its margin. It is small for the size of the animal, reaching about 7 mm in diameter. There are two rows of tentacles along the margin of the oral hood (Figure 4C). The tentacles forming the outer row are all similar in size. The inner row alternates between small, medium, and large tentacles. The largest

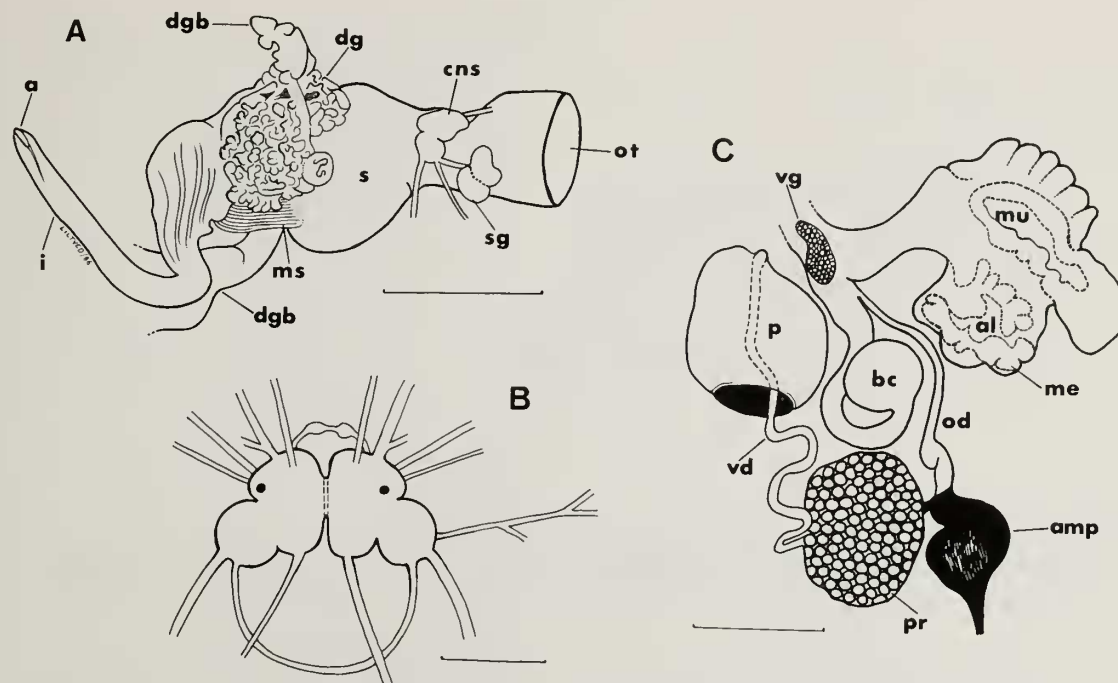


Figure 5

*Melibe megaceras* sp. nov. A. Digestive system, scale = 2.0 mm. a = anus; cns = central nervous system; dg = digestive gland; dgb = digestive gland branch; i = intestine; ms = muscular portion of stomach; ot = oral tube; s = stomach; sg = salivary gland. B. Central nervous system, scale = 0.5 mm. C. Reproductive system, scale = 1.0 mm. al = albumen gland; amp = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; p = penis; pr = prostate; vd = vas deferens; vg = vaginal glands.

tentacles of this row are larger than those forming the outer row. The rhinophore sheath (Figure 8G) is tall and cylindrical. At its posterior apex is a single elongate appendage. The rhinophores are perfoliate, consisting of 7–9 lamellae. There are 5 or 6 elongate cerata along either side of the body. The longest are the anteriormost, which may reach 25 mm in length. Each ceras (Figure 9F) terminates in 1–5 elongate apices, which may equal the basal portion of the ceras in their length. Numerous unbranched papillae are situated around the body. From 8 to 17 of these papillae are randomly distributed on the dorsal surface of the oral hood. Another 11–20 papillae are situated along either side of the notum and 6–9 papillae are present along either side of the body. The anus (Figure 4A) is situated between the first and second cerata of the right side of the body. The nephroproct is located immediately dorsal to the anus. The single gonopore is ventral to the anteriormost ceras. The foot is narrow, about 6 mm in width. Its anterior margin is rounded and entire.

**Digestive system** (Figure 5A): The buccal mass is broad and muscular, without any jaws or radula, in the five specimens dissected. A fold where the jaws are usually situated is devoid of any chitinous tissue. There is a single globular salivary gland on either side of the buccal mass. The esophagus is exceedingly short and expands abruptly into the saccate stomach. The posterior half of the stomach

is lined with approximately 20 chitinous plates (Figure 10E), which are highest posteriorly. The digestive gland is situated largely on the dorsal surface of the stomach. A tubule of dense digestive gland tissue enters both of the anteriormost cerata. Emerging from the bifurcation of the left digestive gland is a duct that leads posteriorly to the diffuse digestive gland, which interdigitates with the ootestis. A portion of this diffuse digestive gland enters the base of each of the posterior cerata. The intestine emerges from the posterior end of the stomach, bends ventrally, and recurves dorsally to the anal opening.

**Central nervous system** (Figure 5B): The cerebral and pleural ganglia are almost entirely fused. The pedal ganglia are smaller than the cerebral and pleural ganglia and are connected by an elongate commissure. The buccal ganglia are situated on the ventral surface of the buccal mass and are joined to the cerebral ganglia by thin, short nerves. The eyes are situated on short nerves that join the dorsal surface of the cerebral ganglia.

**Reproductive system** (Figure 5C): The ampulla is S-shaped and black in color in the five specimens examined. The pigment was retained in specimens, regardless of the preservative in which they were placed; thus it is not a fixation artifact. At its distal end the ampulla bifurcates into the vas deferens and the oviduct. The oviduct is thick and muscular and joins the female gland mass and bursa

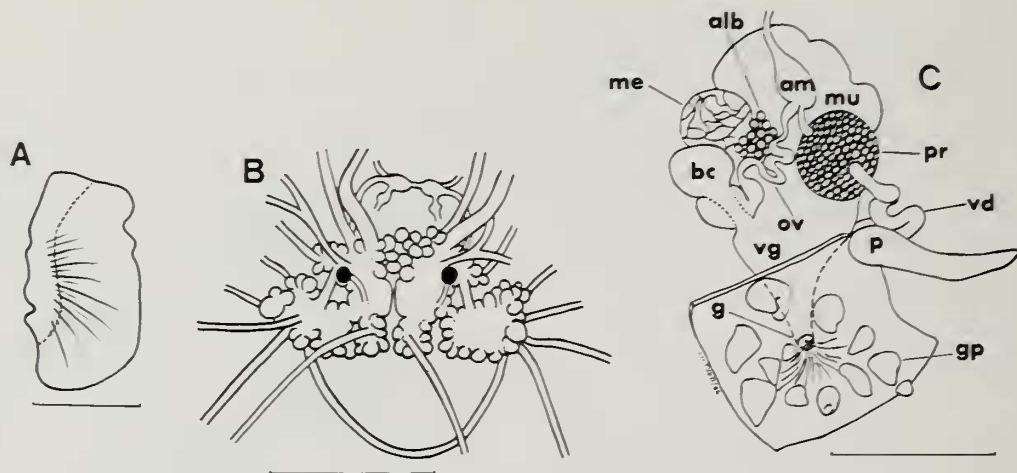


Figure 6

*Melibe pilosa* Pease, 1860. A. Jaw, scale = 0.25 mm. B. Central nervous system, scale = 1.0 mm. C. Reproductive system, scale = 2.0 mm. alb = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; ov = oviduct; p = penis; pr = prostate; vd = vas deferens; vg = vaginal glands.

copulatrix near the single gonopore. The largest portion of the female gland mass is the mucous gland. The albumen and membrane glands are approximately the same size. The spherical bursa copulatrix joins the oviduct and female glands by means of a thick, elongate duct. There is a small, pyriform glandular area at the junction of the three female ducts. The vas deferens, following its origin from the ampulla, expands into a large prostate gland, consisting of numerous follicles. At the distal end of the prostate the vas deferens narrows into a muscular ejaculatory segment, containing a few convolutions. Here the vas deferens enters the paddle-shaped penis and terminates at the common gonopore.

**Natural history:** Specimens of *Melibe megaceras* have been found on shallow-water sand flats and may be seasonally common. Specimens in Kaneohe Bay were found sympatrically with *M. pilosa*. When actively crawling, the cerata are held horizontally and the animal is exceedingly flat. The translucent brownish color with opaque white spots makes this animal virtually invisible on a sandy substratum. Fragments of small crustaceans were present in the feces (Steve Kempf, personal communication). When disturbed the animals swim by means of rapid, lateral flexure of the body.

**Development:** The white egg mass is a broad, coiled ribbon that is attached to the sand substratum by a mucous thread. There are 1–3 eggs per capsule. The zygotes are 72  $\mu\text{m}$  in diameter. From oviposition to hatching at 24–26°C requires 3 days. The shell of the planktotrophic larvae is 128  $\mu\text{m}$  in length and is type-1. Development times and measurements were provided by Steve Kempf (personal communication).

**Distribution:** Specimens of *Melibe megaceras* have been found on several occasions within Kaneohe Bay, Oahu. A few specimens have been collected from Kauai and Maui (Steve Kempf, personal communication). This species is not known outside the Hawaiian Islands, but this may be a result of its cryptic appearance.

*Melibe pilosa* Pease, 1860

(Figures 1D, 6, 8H, 9I, 10H, 11A)

*Melibe pilosa* PEASE, 1860:34.

*Jacunia papillosa* DE FILIPPI, 1867:233; ODHNER, 1936:1116.

*Melibe vexillifera* BERGH, 1880:162, pl. 2, figs. 1–11, pl. 3, figs. 1–3; ODHNER, 1936:1116.

**Material:** California Academy of Sciences, San Francisco, CASIZ 061506, one specimen, intertidal, Diamond Head Beach Park, Oahu, Hawaii, 8 February 1986, Michael T. Ghiselin. CASIZ 061501, one specimen, 2 m depth, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 10 February 1986, Terrence M. Gosliner. CASIZ 061505, one specimen, Inhaca Island, Mozambique, July 1935, William Macnae.

**Description: External morphology:** The preserved specimens range from 30 to 120 mm in length. Living animals (Figure 1D) are translucent white with various amounts of brown pigment, owing to the presence of symbiotic zooxanthellae. Large, isolated spots of dark brown may be present on the cerata. Scattered small spots of opaque white are distributed over most of the body's surface. The oral hood is entire, circular, and of moderate diameter. There are four rows of tentacles along the margin of the oral hood, with the innermost row containing the longest ones. The rhinophore sheath (Figure 8H) widens near its



free end. Several papillae are present along the posterior margin of the sheath, including a multifid papilla at the posterior apex. The perfoliate rhinophores possess 9–11 lamellae. The triangular cerata (Figure 9I) are arranged in alternating rows with 5–8 cerata per side. The cerata have numerous elongate papillae scattered over their surfaces. Similar unbranched or branched papillae are present on the notum and sides of the animal. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is directly anterior to the anus. The gonopore is situated ventral to the anteriormost ceras and is surrounded by several conical papillae. The foot is narrow and rounded anteriorly.

**Digestive system:** The thick muscular buccal mass contains a pair of jaws (Figures 6A, 11A) with approximately 35 irregular denticles along the elongate masticatory border. A radula is entirely absent. The esophagus is elongate and wide, widening even more posteriorly, where it expands to form the stomach. The stomach is muscular posteriorly and contains 16–30 narrow, laterally compressed chitinous plates (Figure 10H). The arrangement of the branches of the digestive gland is identical to that described for *Melibe liltvedi*, except that the digestive gland is more highly branched, with finer tubules.

**Central nervous system** (Figure 6B): The arrangement of the ganglia is identical to that described above for other members of the genus. The major morphological difference is that all of the dorsal ganglia of *Melibe pilosa* have a highly nodular appearance, owing to the fact that most of the large neuronal cells are located peripherally on the ganglia. The buccal ganglia are rounded in appearance and possess smaller peripheral ganglia near the major buccal bodies.

**Reproductive system** (Figure 6C): The ampulla is short and saccate, branching distally into the oviduct and vas deferens. The oviduct is narrow and highly convoluted. It joins the female atrium at a glandular expansion at the base of the bursa copulatrix. This gland is circular and situated at the proximal end of the female atrium. The bursa copulatrix is short and spherical. The female gland mass is composed of the yellow follicular albumen gland, the sinuous membrane gland, and the large, smooth mucous gland. A short distance from the bifurcation of the ampulla, the vas deferens enters the spherical prostate. The prostate consists of numerous small spherical bodies. The vas deferens emerges again from the distal portion of the prostate as a thicker ejaculatory duct. It expands into the conical, unarmed penis.

**Natural history:** Specimens have been found commonly in the Hawaiian Islands (present study), where they inhabit intertidal and shallow subtidal reef and sand flats. The animals are very cryptic on mixed sand, rock, and algal substrata. The single specimen from Mozambique examined in this study contained a gravid female portunid crab in its stomach. The egg mass consists of several whorls (BERTSCH & JOHNSON, 1981).

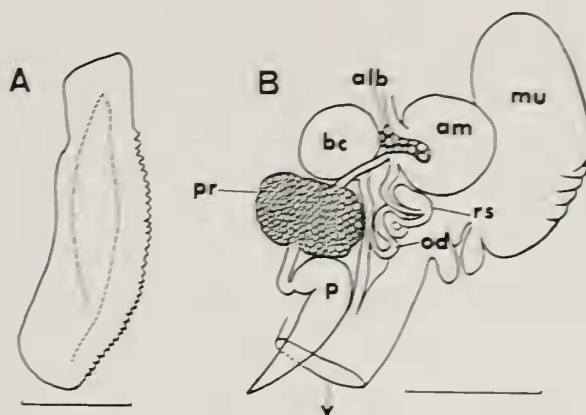


Figure 7

*Melibe rosea* Rang. 1829. A. Jaw. 0.25 mm. B. Reproductive system. scale = 1.0 mm. alb = albumen gland; am = ampulla; bc = bursa copulatrix; mu = mucous gland; od = oviduct; p = penis; pr = prostate; rs = receptaculum seminis; v = vagina.

*Melibe rosea* Rang. 1829

(Figures 1E, 7, 8J, 9J, 10J, 11B)

*Melibe rosea* RANG. 1829:130. pl. 3. fig. 3.

**Material examined:** SAM A33980, four specimens, collected intertidally under rocks, Dale Brook, False Bay, Cape Province, South Africa, 18 November 1979, T. M. Gosliner. CASIZ 061503, two specimens, 10 m depth, Phillips Reef, Algoa Bay, Cape Province, South Africa, 14 May 1984, W. R. Liltved.

**Description: External morphology:** The preserved animals range from 6 to 80 mm in length. The living animals (Figure 1E) are uniformly light rose pink to orange. Frequently a linear swath of opaque white pigment may be present on the notum, between the cerata and extending on to the bases of the cerata. Most of the surface of the animal is covered with small rounded tubercles. The circular oral hood is entire along its margin. There are 2 or 3 rows of papillae along the margin of the oral hood. There are 3 rows of papillae along the posterior half of the oral hood, which diminish to 2 rows in the anterior half of the hood. The innermost papillae are the thickest and longest. The rhinophore sheaths (Figure 8J) are rounded apically, without any papillae. The perfoliate rhinophores possess 5–9 lamellae. There are 6 or 7 cerata on either side of the body. Each ceras (Figure 9J) is pyriform with dense rounded tubercles, giving the entire ceras a nodular appearance. The anteriormost cerata are largest. The anus is situated directly anterior to the second ceras on the right side. The nephroproct is immediately dorsal to the anus. The gonopore is ventral to the anteriormost ceras. The foot is narrow and rounded anteriorly.

**Digestive system:** The buccal mass is thick and muscular. The chitinous jaws (Figure 7A, 11B) have a mas-



Table 1  
Morphology of species of *Melibe*.

Species	Distribution	Jaws	Rhinophore sheaths	Oral hood	Stomach plates	Penis	References
<i>M. australis</i> (Angas, 1864)	New South Wales, Victoria, Australia	absent	simple without papillae	with single row of tentacles	unknown	unknown	ALLAN, 1932; BURN, 1957; THOMPSON, 1972
<i>M. bucephala</i> Bergh, 1902	Thailand, Red Sea	small with undulate margin	flattened leaf-like	incised anteriorly, 5 rows of tentacles innermost longest	20	large conical	BERGH, 1902; O'DONOGHUE, 1929
<i>M. capucina</i> Bergh, 1875	Cebu, Philippines	with 22 or 23 coarse denticles	small simple without papillae	4 rows of tentacles	10	simple conical	BERGH, 1875
<i>M. engeli</i> Risbec, 1937	New Caledonia	with small denticles	flattened with large papillae	2 rows	12	broad conical	RISBEC, 1937, 1953
<i>M. fimbriata</i> Alder & Hancock, 1864	Zanzibar, India, Japan, Mediterranean	thin cuticular	simple without papillae	incised anteriorly, outer row shortest	28	elongate	ALDER & HANCOCK, 1864; ELIOT, 1902, 1913; THOMPSON & CRAMPTON, 1984
<i>M. japonica</i> Eliot, 1913	Japan	with undulate margin	simple with posterior tubercle	2 or 3 rows posteriorly, 9 or 10 rows of tentacles	24	"broad"	ELIOT, 1913; BABA, 1949
<i>M. leonina</i> (Gould, 1852)	Alaska to Baja California	absent	flattened leaf-like	2 rows of tentacles, outer rows longer	absent	elongate flattened	ODHNER, 1936; MACFARLAND, 1966; present study
<i>M. liltvedi</i> sp. nov.	Atlantic Ocean, southern Africa	absent	simple with posterior papilla	2 or 3 rows of tentacles	5 or 6	elongate conical	present study
<i>M. maugaeana</i> Burn, 1960	Victoria, Australia	unknown	with posterior papillate margin	single row of tentacles	unknown	unknown	BURN, 1957, 1960
<i>M. megaceras</i> sp. nov.	Hawaiian Islands	absent	with elongate posterior papilla	2 rows, inner row longer but alternating	20-24	broad spatulate	present study
<i>M. mirifica</i> (Allan, 1932)	Queensland, Australia	with undulate margin	simple funnel-shaped	incised anteriorly, 4 rows of tentacles	about 40	unknown	ALLAN, 1932; WILLAN & COLEMAN, 1984
<i>M. ocellata</i> Bergh, 1888	Indian Ocean, Polo-Edam	smooth	unknown	2 or 3 rows of tentacles	24	conical	BERGH, 1888
<i>M. pilosa</i> Pease, 1860	Mozambique-Hawaii	with undulate margin	with 1-3 posterior papillae	4 rows of tentacles, inner row longest	about 30, 16-20 present study	conical	ODHNER, 1936; EDMUNDS & THOMPSON, 1972; present study
<i>M. rangi</i> Bergh, 1875	Red Sea	25-30 denticles	with posterior papilla	2 rows of tentacles	26-31	broad conical	BERGH, 1875
<i>M. rosea</i> Rang, 1829	temperate South Africa	large with 22 denticles	simple without papillae	2 or 3 rows posteriorly, 2 rows anteriorly but subequal	7-8	elongate conical	BERGH, 1907; THOMPSON & CRAMPTON, 1984; present study

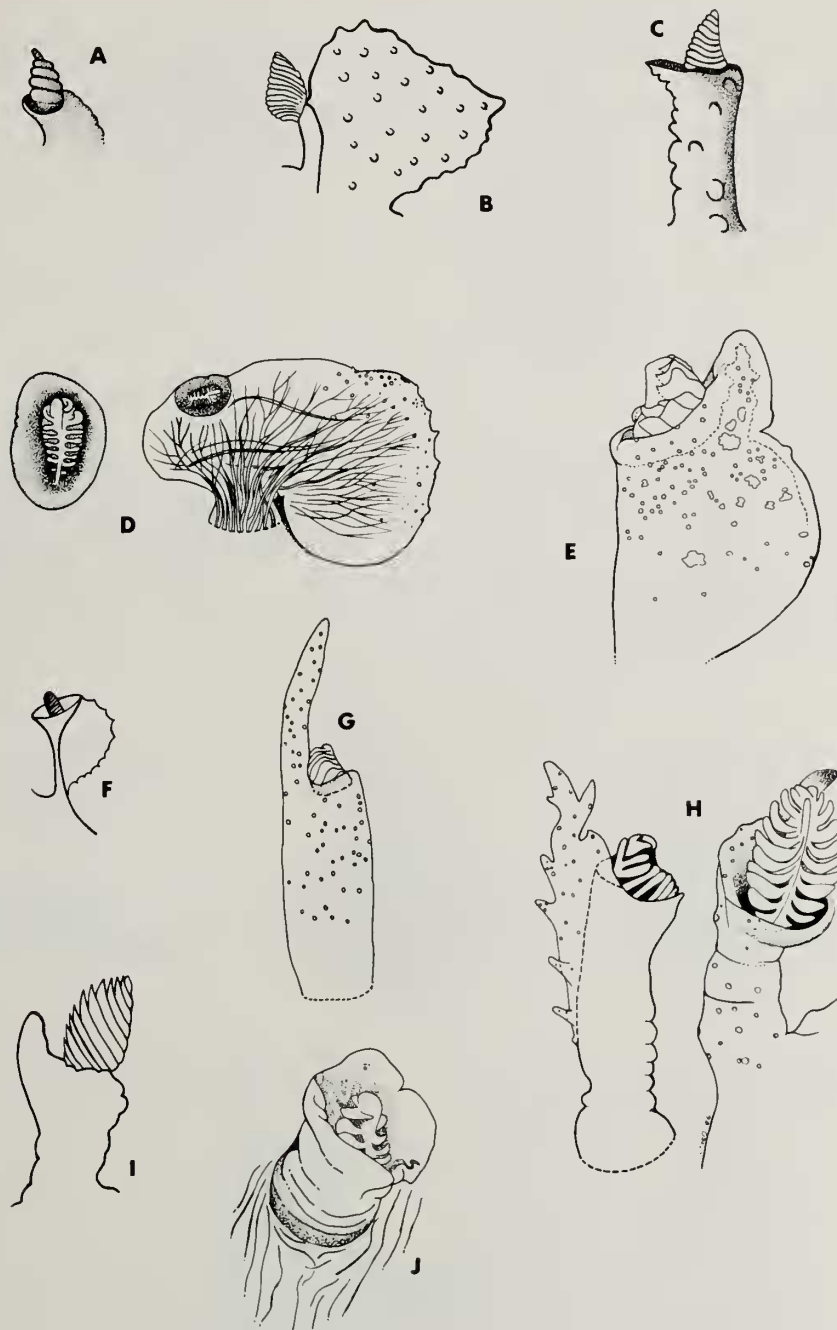


Figure 8

Rhinophores of *Melibe*. A. *Melibe australis* (Angas, 1864) (after THOMPSON, 1972). B. *M. bucephala* Bergh, 1902 (after O'DONOGHUE, 1929). C. *M. fimbriata* Alder & Hancock, 1864 (after THOMPSON & CRAMPTON, 1984). D. *M. leonina* (Gould, 1852). E. *M. liltvedi* sp. nov. F. *M. maugeana* Burn, 1960 (after BURN, 1957). G. *M. megaceras* sp. nov. H. *M. pilosa* Pease, 1860. I. *M. rangi* Bergh, 1875 (after BERGH, 1875). J. *M. rosea* Rang, 1829.

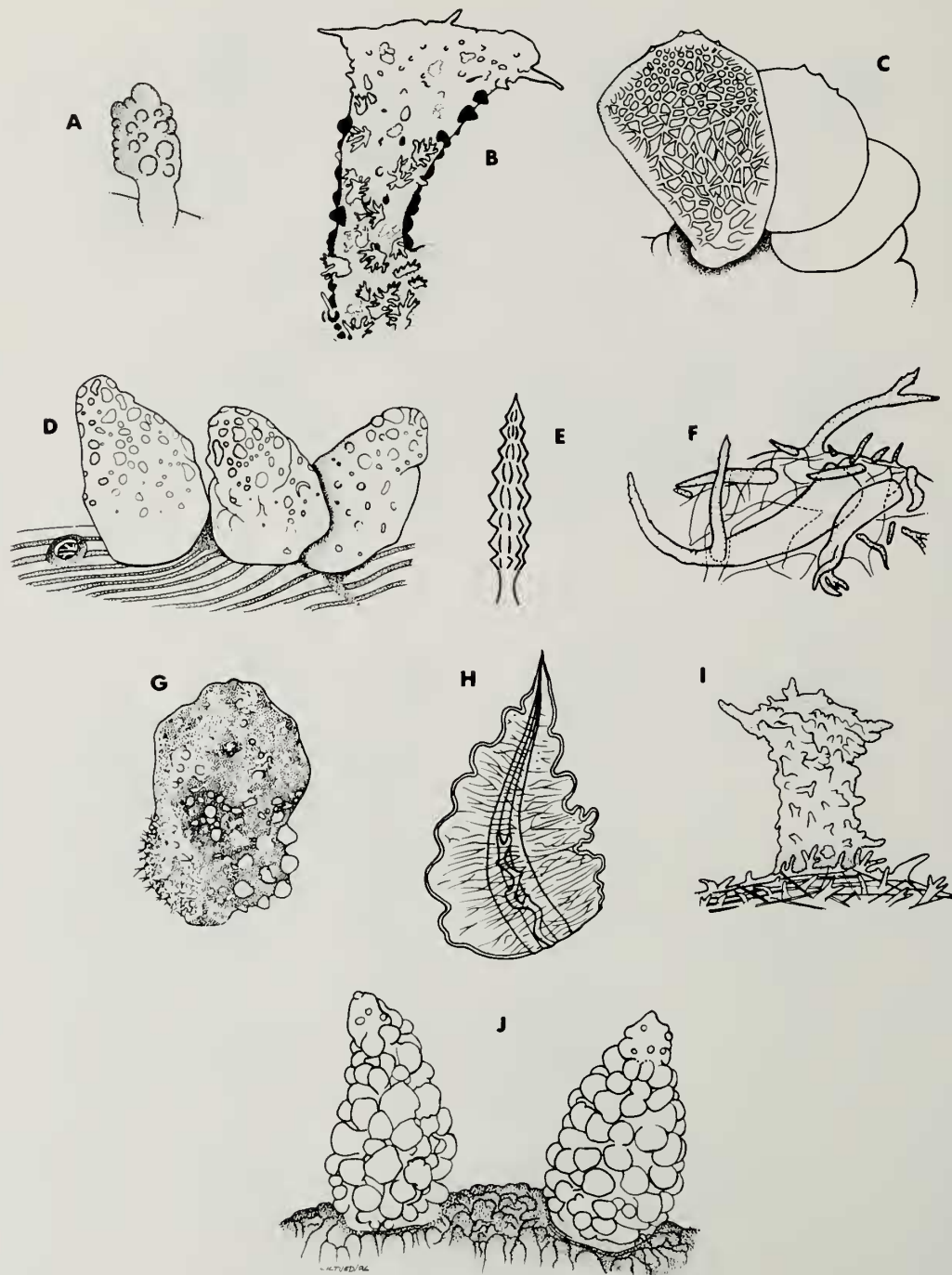


Figure 9

Cerata of *Melibe*. A. *Melibe australis* (Angas, 1864) (after THOMPSON, 1972). B. *M. fimbriata* Alder & Hancock, 1864 (after THOMPSON & CRAMPTON, 1984). C. *M. leonina* (Gould, 1852). D. *M. liltvedi* sp. nov. E. *M. maugéana* Burn, 1960 (after BURN, 1957). F. *M. megaceras* sp. nov. G. *M. mirifica* (Allan, 1932) (after ALLAN, 1932). H. *M. ocellata* Bergh, 1888 (after BERGH, 1888). I. *M. pilosa* Pease, 1860. J. *M. rosea* Rang, 1829.

tatory border containing 22 denticles in one specimen observed. A radula is entirely absent. The remainder of the digestive system is virtually identical to that described

for *Melibe liltvedi* with one notable exception. In *M. rosea*, 7 or 8 chitinous plates are within the stomach (Figure 10J).



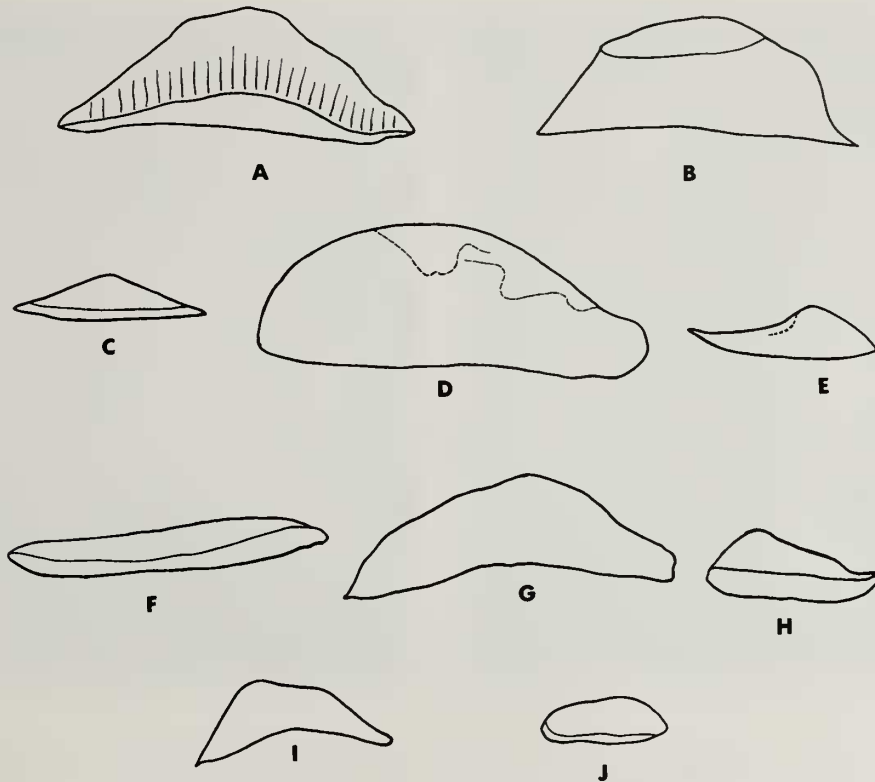


Figure 10

Stomach plates of *Melibe*. A. *Melibe bucephala* Bergh, 1902 (after BERGH, 1902). B. *M. capucina* Bergh, 1875 (after BERGH, 1875). C. *M. fimbriata* Alder & Hancock, 1864 (after THOMPSON & CRAMPTON, 1984). D. *M. liltvedi* sp. nov. E. *M. megaceras* sp. nov. F. *M. mirifica* (Allan, 1932) (after ALLAN, 1932). G. *M. ocellata* Bergh, 1888 (after BERGH, 1888). H. *M. pilosa* Pease, 1860. I. *M. rangi* Bergh, 1875 (after BERGH, 1875). J. *M. rosea* Rang, 1829.

**Central nervous system:** The arrangement of simply rounded ganglia is identical to that described for *Melibe liltvedi* and *M. megaceras*.

**Reproductive system** (Figure 7B): The narrow preampullary duct widens into the short, curved ampulla. The ampulla narrows again and divides into the vas deferens and oviduct. The oviduct is thick and convoluted. At its proximal end is an expanded muscular portion, which probably functions as a receptaculum seminis. More distally the oviduct enters the duct of the bursa copulatrix near the middle or at the base of the bursa duct. The duct of the spherical bursa copulatrix is elongate, almost half of the length of the entire genital mass. The albumen gland is a small tightly convoluted mass. The membrane gland is slightly larger and consists of larger folds. The mucous gland is the largest portion of the genital mass and is folded several times. The vas deferens enters the spherical prostate after a moderate distance. The prostate consists of numerous small glandular spheres. From its distal end the muscular vas deferens emerges again and widens into the conical, unarmed penis.

**Natural history:** Specimens commonly have been found under rocks in the mid-intertidal zone to a depth of 10 m. The specimens were in the open rarely during the day and are likely to be nocturnal.

**Distribution:** This species appears to be endemic to southern Africa and has been found on the Atlantic coast from Port Nolloth to Port Alfred on the Indian Ocean.

## DISCUSSION

The Tethyidae are dendronotacean nudibranchs with an expanded oral hood that is used to capture crustacean prey. In *Fimbria*, the oral hood is less well developed and accessory gills are present at the base of the cerata. The external morphology of *Melibe* is conservative (Table 1). All known species possess an oral hood with 1–10 rows of tentacles around the margin, 4–9 cerata per side, an anus and nephroproct anterior to the second ceras, and a gonopore ventral to the first ceras.

The oral hood is indented anteriorly in *Melibe fimbriata*, *M. mirifica*, *M. japonica*, and *M. bucephala*, but is entire

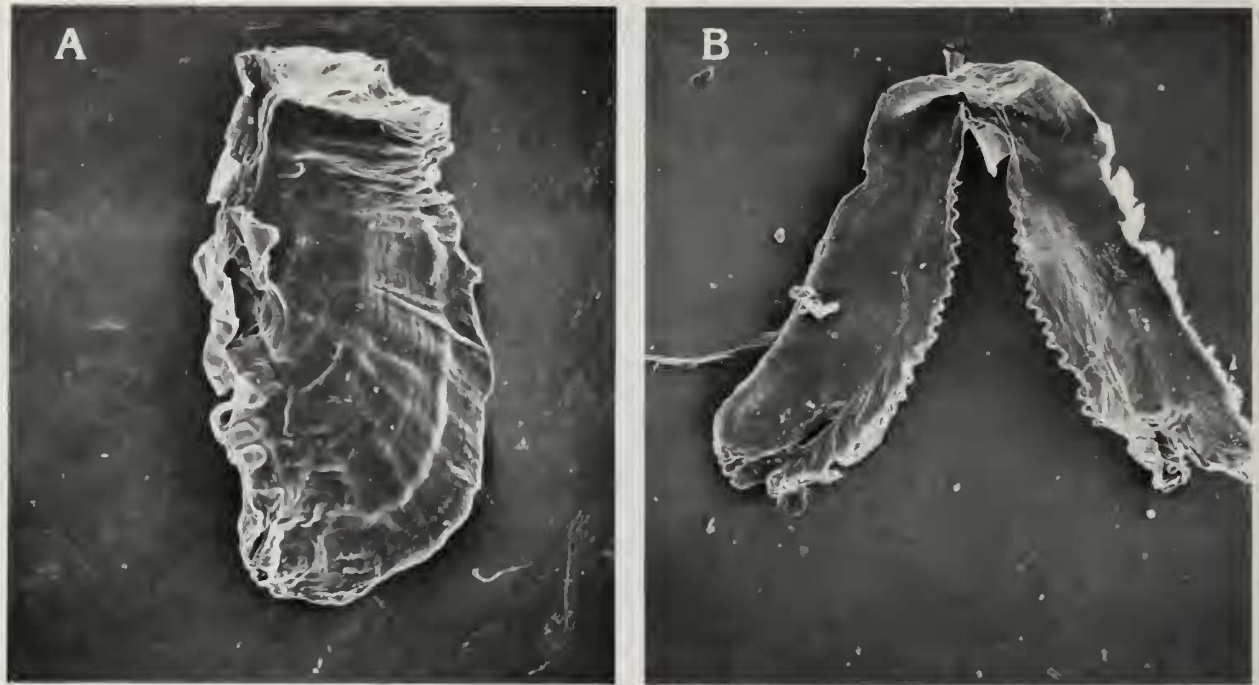


Figure 11

Scanning electron micrographs of jaws. A. *Melibe pilosa* Pease, 1860,  $\times 110$ . B. *M. rosea* Rang, 1829,  $\times 60$ .

in the remaining species. The number of rows of tentacles and their relative lengths differ significantly among species (Table 1). *Melibe liltvedi* has alternately large medium and small tentacles forming the inner row of the oral hood. The elaboration of the rhinophore sheaths differs considerably among species (Figure 8). *Melibe leonina* (Gould, 1852), *M. bucephala* Bergh, 1902, *M. engeli* Risbec, 1937, and *M. maugeana* Burn, 1960 (a new name proposed by Burn for *M. pellucida* Burn, 1957, which is a junior homonym of *M. pellucida* Bergh, 1904) have broad flattened rhinophore sheaths, whereas they are cylindrical or funnel-shaped in the remaining species. In some species, *M. rangi* Bergh, 1875, *M. liltvedi*, *M. megaceras*, and *M. pilosa* Pease, 1860, the rhinophore sheath may bear papillae on its posterior margin. In *M. megaceras* the rhinophoral papilla is elongate, almost equaling the remainder of the sheath in its length.

The shape of the cerata may vary considerably among species of *Melibe* (Figure 9). *Melibe ocellata* Bergh, 1888, and *M. rangi* Bergh, 1875, are the only species known to possess acutely pointed cerata. *Melibe rosea* Rang, 1829, *M. australis* (Angas, 1864) and *M. liltvedi* all have rounded tuberculate cerata, similar in appearance to those found in species of *Doto*. In *M. fimbriata*, *M. engeli*, *M. japonica*, *M. mirifica*, *M. bucephala*, and *M. pilosa* the cerata are wedge-shaped with numerous tubercles or papillae, some of which may be highly ramified. The cerata of *M. mau-*

*geana* are acutely pointed with several distinct rows of tubercles. In *M. megaceras* the cerata have 1–5 acutely pointed apices. The cerata of *M. leonina* are flattened and foliaceous.

The notum is smooth in *Melibe leonina*, *M. maugeana*, and *M. liltvedi* and tuberculate to papillate in the remaining species.

A radula is absent in all members of the genus, although jaws may be present in some species and absent in others. Jaws are absent in *Melibe australis*, *M. leonina*, *M. liltvedi*, and *M. megaceras*. Distinct denticles may be present along the masticatory border of the jaws of *M. capucina*, *M. engeli*, *M. rangi*, and *M. rosea*, whereas the border is undulate or smooth in the remaining species. The esophagus is short in most species but is far more elongate in *M. pilosa* (present study).

A series of chitinous gastric plates is present in the posterior portion of the stomach of all species of *Melibe*, with the exception of *M. leonina*, where they are entirely wanting. The number of plates varies intraspecifically, but *M. rosea*, *M. capucina*, *M. engeli*, and *M. liltvedi* have far fewer plates than do other species. The shape of the plates is somewhat variable, but some species such as *M. megaceras* have plates of a consistently distinct shape (Figure 10).

Most of the digestive gland tissue of *Melibe megaceras* is concentrated around the stomach. In all other species

where it is known, the digestive gland is distributed far more evenly in the posterior portion of the body, where it interdigitates with the ovotestis.

The relative shape of the ganglia forming the central nervous system varies somewhat among species. In *Melibe japonica* and *M. pilosa* the ganglia have a nodular appearance owing to the presence of peripheral nerve cells (ELIOT, 1913; present study). In *M. leonina* the cerebral ganglia are bilobed anteriorly with prominent medial lobes. In the remaining species that have been studied all the ganglia are uniformly rounded.

The reproductive morphology varies within *Melibe*, but has not been described fully in the majority of species. The entire genital mass of *M. leonina* is elongate (MACFARLAND, 1966; present study), but forms a distinct genital mass in the other species where it has been described. The ampulla of *M. megaceras* is black in all specimens examined. BERGH (1875) described the presence of a fan-shaped organ in *M. rangi*. This represents a dilation that contains numerous convolutions or lobes of the oviduct and may function as a receptaculum seminis. This expansion of the oviduct was evident in most species of *Melibe* examined in this study but was most pronounced in specimens of *M. liltvedi* and *M. rosea*. It is also illustrated for *M. leonina* (MACFARLAND, 1966:pl. 54, fig. 1). In other species the oviducal folds are not contained in a distinct dilation. The relative position and elaboration of the bursa copulatrix also seems to vary intraspecifically. *Melibe pilosa* and *M. megaceras* are the only described species that have a dilated vaginal atrium. They also possess a discrete mass of vaginal glands near the gonopore. The relative size of the glandular bodies forming the prostate varies interspecifically and may be useful in separating closely allied species. The penis is conical in most species but is broad and spatulate in *M. megaceras*.

Comparison of several similar taxa is difficult owing to incomplete descriptions or inadequate attention to intraspecific variability. WILLAN & COLEMAN (1984) suggested that *Melibe mirifica* (Allan, 1932) may be synonymous with *M. japonica* Eliot, 1913. The external body form of *M. fimbriata* Alder & Hancock, 1864, is also similar to the above taxa, as all three taxa have an indented anterior margin of the oral veil and papillate cerata. Although it is likely that the three species may in fact be synonymous, inadequate material and incomplete descriptions prevent a detailed comparison at this time. *Melibe bucephala* can be readily differentiated from the other species with an indented anterior margin of the oral hood by its broad rhinophore sheath with an undulating posterior margin. *Melibe capucina*, *M. engeli*, *M. japonica*, *M. ocellata*, and *M. rangi* are known only from the descriptions of preserved material. Their status is open to question until further comparative material is available.

The two species of *Melibe* described here can be readily distinguished from all other previously described species. *Melibe liltvedi* is most closely allied to *M. rosea* and *M. australis*. All three taxa have *Doto*-like cerata and are found

only in southern oceans. There are several consistent morphological differences that distinguish these species. *Melibe australis* bears only a single row of tentacles around the margin of the oral hood, while *M. rosea* and *M. liltvedi* have 2 or 3 rows. *Melibe liltvedi* has a triangular extension on the posterior end of the rhinophore sheath that is absent in the other two species. There are numerous elongate dendritic papillae along the medial portion of the notum in *M. australis*. In *M. rosea* there are scattered simple tubercles over the entire body while in *M. liltvedi* the body surface is entirely smooth. The number of cerata per side of the body differs between the three species. In *M. australis* there are 4 or 5 rows, in *M. liltvedi* 5 or 6 rows, and in *M. rosea* 6 or 7 rows. These differences are not size dependent. The cerata of *M. rosea* and *M. liltvedi* are more elongate than those of *M. australis*. There are dense tubercles covering the surface of the cerata in *M. rosea* while in *M. liltvedi* the tubercles are far more scattered. *Melibe liltvedi* is uniformly opaque white in color while the other two species are yellowish, orange, or pink with scattered opaque white pigment.

There are also internal differences that separate these three taxa. *Melibe rosea* has distinct jaws with a well developed, denticulate masticatory border, which are entirely absent in *M. australis* and *M. liltvedi*. There are more stomach plates in *M. rosea* (7 or 8) than in *M. liltvedi* (5 or 6). The stomach plates of *M. australis* are undescribed. The bursa copulatrix in *M. rosea* is spherical, with an elongate duct, while in *M. liltvedi* it is small and pyriform, with a short duct. These differences are consistent and are independent of size and maturity. The prostate of *M. rosea* is composed of small glandular bodies while those of *M. liltvedi* are much larger.

*Melibe megaceras* differs markedly from all other described members of the genus. It has elongate cerata with up to five apical branches. It is the only species known to possess a papilla on the posterior end of the rhinophore sheath, which approximates the basal portion of the sheath in length. Internally, it lacks jaws, as in *M. australis*, *M. leonina* and *M. liltvedi*. The digestive gland mass largely surrounds the stomach in *M. megaceras* while in the other species it is far more developed posteriorly. *Melibe megaceras* is the only known species with a broad, spatulate penis and a darkly pigmented ampulla. Together with *M. pilosa*, *M. megaceras* is the only species with a muscular vaginal atrium and vaginal glands. In *M. megaceras* the vaginal glands form a mass on the outer surface of the atrium, while in *M. pilosa* they are located within the atrium.

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